WING MOVEMENTS, HUNTING, AND DISPLAYS OF THE NORTHERN SHRIKE

Tom J. Cade

The recent papers by Selander and Hunter (1960) and by Hailman (1960) on wing-flashing of the Mockingbird (*Mimus polyglottos*) have focused attention on the difficulties of interpreting this kind of behavior. On the one hand, the function of wing-flashing is debated in these two papers; on the other hand, there are important unsettled questions about the origin and the phylogeny of such behavior. Especially important in the latter regard is the degree to which special wing movements in other species may be homologous with the wing-flashing of Mockingbirds. Before these problems can be resolved it will be necessary to have more detailed information, not only on wing-flashing and other types of wing movements in the Mimidae, but also for other passerines with similar types of behavior. It should be particularly rewarding to examine the behavior of other birds that possess conspicuous wing patches like those of *Mimus polyglottos*, to see whether or not such similar morphological features function in analogous ways and to determine to what extent the movements involved in this kind of behavior are the same in the different species.

The Northern Shrike (*Lanius excubitor*) provides an instructive comparison because in several ways it is remarkably like the Mockingbird. The two species are about the same size, and the plumages of the two are similar in general coloration as well as in many details of pattern, including their conspicuous white wing patches. In the Northern Shrike, the white patch appears on the dorsal aspect of the wing distal to the tips of the primary coverts and extends from the first through the seventh primaries. The patch contrasts sharply with the rest of the dorsal surface of the wing. Ventrally the contrast is much less, and the outline of the patch can barely be distinguished. In the Mockingbird, the white patch also appears on the dorsal aspect of the wing distal to the primary coverts but extends from the first through the ninth primaries and also includes one secondary. The coverts of these remiges are also mostly white. The patch therefore covers a larger area of the wing than does the patch on the wing of a shrike. Furthermore, the patch is equally distinct on the ventral and on the dorsal surfaces of the wing of a Mockingbird. The most interesting similarity, however, lies in the fact that the Northern Shrike often uses special wing movements during its hunting forays in a manner which is like the wing-flashing of the Mockingbird.

The purpose of this paper, then, is to describe some wing movements of the Northern Shrike that appear to function in ways analogous to the wing-

flashing of the Mockingbird, to compare these wing movements with others used by shrikes in different behavioral contexts, and finally to compare the wing movements of shrikes and Mockingbirds. These comparisons are made in an effort to discover whether or not homologies exist between the two species with respect to these wing movements and to add to the discussion on the phylogenetic origin of "wing-flashing" movements. Andrew's (1961) important paper on passerine displays provides a general background for the phylogenetic approach.

METHODS

Data on wing movements were obtained in two ways: (1) by observing wild shrikes around their nests in northern Alaska (Lake Peters; Colville River) and on their wintering ground in central New York, and (2) by studying closely the reactions of hand-reared and captive shrikes in various manipulated situations. Daily observations were made on the behavior of a pair of shrikes nesting at Lake Peters in 1960, and again in 1961, and less intensive observations were made on the actions of shrikes around 17 other nests at various localities north of the Brooks Range in the years 1958 to 1961. Many instances of special wing movements were recorded at these nests. Since 1959, 19 captive shrikes have been under study. Eleven of these were hand-reared nestlings, four of which were under observation for more than a year; and eight were trapped as adults or immatures in the winter around Syracuse, New York. One of the latter was also under observation for more than a year.

Most of the wing movements observed around nests were elicited under natural circumstances—consisting of reactions to potential nest predators, or to prey, and of social interactions between mates. A few tests were carried out in 1961 by placing stuffed shrikes and other dummies near nests. Wintering shrikes have been tested with dummies and by placing live, captive shrikes in their hunting areas.

The captives, on the other hand, were repeatedly subjected to experimentation. Primary consideration was given to testing the reactions of the shrikes to various kinds of live prey introduced into their cages and to testing their interactions with each other. But their responses to cats and dogs, stuffed hawks and owls, and to "strange objects" such as children's toys, have also afforded instances of special wing movements.

Finally, two hand-reared shrikes were trained by a slight modification of the techniques used in falconry to fly free out-of-doors, to hunt, and to return on call to a portable cage made of splintered bamboo. One of these birds was flown almost daily for more than a year and a half. These trained birds provided many instances of special wing movements while hunting or during hostile encounters with other species.

DESCRIPTION OF WING MOVEMENTS AND OBSERVATIONS

Special wing movements by shrikes occur in many different behavioral contexts, but these can be grouped into six categories for comparative purposes: (1) flight-intention movements, (2) food-begging by young, (3) courtship displays, (4) hunting tactics, (5) hostile reactions to enemies or to other, large species, and (6) stretching reflexes. The last-mentioned will not be considered in this paper, and food-begging is so similar to the familiar pattern observed in passerines that it need not be dealt with as a special topic.

FLIGHT-INTENTION MOVEMENTS

Description.—Flight-intention movements have been the subject of a good deal of ethological discussion (Daanje, 1950; Andrew, 1956), and the behavior is probably universal among flying birds; but the pattern of movements is not the same in all species. For instance, Andrew (1956) distinguishes four basic types of tail-flicks used by passerines in flight-intention.

Northern Shrikes indicate their intention to fly by stereotyped, readily recognizable patterns of behavior, one of the most characteristic components of which is a rapid flicking of the wings away from the body and back to it. Typically, these flicks are initiated from a normally folded position of the wings, and the movement, which is most conspicuous at the bend of the wing (carpus), appears to result mainly from rapid, partial extension and flexion of the forearm with simultaneous abduction and adduction of the humerus. Flipping the tail (down-up type) parallel with the median plane of the body often precedes the wing-flicks and, when executed alone, is the weakest expression of flight-intention given by shrikes. As the tendency to fly increases, the wing-flicks and tail-flips occur together, and the tail may also be spread and closed as it is flipped, particularly if aggressive tendencies are also present. These movements are performed in a more or less normal, upright sitting position with the plumage slightly sleeked. Ruffed plumage may occur if hostile tendencies are present. In its most intense expression, flight-intention also includes various bobbing and twisting movements of the body, which is oriented in the horizontal plane, with the tail being flipped rapidly down and up or rotated quickly from side to side in synchrony with the wing-flicks. The plumage is extremely sleeked, except when aggressive tendencies are present, giving the bird a long, thin appearance. Such extreme movements are most often performed during "conflict" situations—for instance, when a shrike encounters nest predators or strange animals, when it spots quarry that may present difficulties of capture (large rodent), or when it sees tempting prey but is not highly motivated to hunt. Sometimes a very

striking display is produced with the white wing patches and the white parts of the tail feathers both "flashing" conspicuously.

Typical observations.—12 February 1961. Example of low intensity movements. An immature shrike was observed near Cicero, Onondaga County, New York, sitting in the top of an elm tree about 60 feet above the ground, which was covered with deep snow. I set a balchatri trap (see Cade, 1955; Berger and Mueller, 1958) baited with a live canary on the snow about 350 yards from the shrike. As soon as I withdrew to my car, 50 yards from the trap, the shrike flew toward the trap but stopped about 50 yards short and flew into a small willow tree, where it chased a Blue Jay (*Cyanocitta cristata*), which I had not previously seen. The jay flew away, and the shrike sat on a low branch of the tree about 5 feet above the ground intently watching the canary. The shrike apparently was not very hungry, because it sat in the same place for nearly 10 minutes watching the trap and occasionally flipping its tail down and up. Finally it flew toward the trap but alighted on the snow and hopped all around the trap instead of landing on top of it. Then the shrike jumped up into the air and hovered about a foot over the trap for several seconds before flying off to land in a small bush about 10 yards away from the trap. There it perched in a horizontal position facing the trap with the tail flipping and the wings flicking off and on for a minute or more. Then the shrike flew back to the trap and hovered over it again but did not land. Slight variations of this performance continued for about 10 minutes before the shrike finally lost interest and flew away.

15 January 1960. Example of high intensity movements. A captive, adult female shrike was taken into a living room where a full-grown house cat was sleeping on the hearth. This shrike was tame enough to sit quietly on my finger. I stood in the middle of the room holding the shrike on my finger about 5 feet above the floor. The cat was then awakened, and as soon as she began to stretch and move a little, the shrike immediately sleeked down her plumage to an extreme degree and assumed a rigid, upright posture. As the cat moved around the room, the shrike turned her head to follow but otherwise remained motionless. The cat did not stalk the strike or approach closely. Gradually the strike began to relax her plumage and appeared to become "alert" and "curious" about the actions of the cat. Soon her tail began flipping, followed shortly after by wing-flicks. I then called the cat to my feet, the shrike still being perched on my finger 5 feet above the floor. As the cat approached, the strike became active on my finger, constantly shifting the position of her feet. She moved into a horizontal position and started screaming a series of *jaa* calls, which wild shrikes use in the presence of mammalian predators at their nests. Occasionally an alarm whistle was also uttered, and the shrike began twisting and bobbing her body rapidly, at the same time quickly spreading and closing her tail and flicking her wings as she looked down at the cat below. The cat was then removed from the room, and the shrike soon quieted down, although she remained sleeked and alert for several minutes after.

COURTSHIP DISPLAYS

Description.—Quivering and fluttering movements of the wings are used by male and female shrikes in many of their social interactions during the breeding season. I have not yet observed the complete sequence of courtship displays in the wild, but captive pairs in large, indoor flight rooms have given a good many hints about what probably takes place. Only details pertinent to the present topic are presented here.

Most of the displays involving wing movements are concerned with some expression of the tendency to engage in courtship-feeding, which is the main interaction between male and female shrikes during the preincubation phase of the breeding cycle. The male, when presenting food to his mate, quivers or flutters his wings and utters a call note, which phonetically is *wuut*. The call sounds the same as the note which males and females use when they land on the rim of the nest with food for the young. The female, when soliciting for food from her mate, also quivers or flutters her wings and utters a whining note like *waik, waik* repeated over and over. This sound is much like the food-begging whine of the nestling or, especially, the fledgling shrike. A single, captive male with developed gonads will often take a bite of meat in his beak and hop about over all the perches in his room, fluttering his wings (wing patches make conspicuous flashes) and uttering *wuut* sounds. These activities are usually interspersed with periods of singing. Likewise, a single, captive female with developing gonads will often sit fluffed out on a branch in her room, quivering her wings and calling *waik*. This behavior is also interspersed with singing. Captive females readily learn to associate their keeper with food and will give this display when he enters the room with meat in his hand.

Males also quiver or flutter their wings quite often when they are singing, and there is a special, upright bill-raising display given by males and females —often during song—in which the wings are quivered, the tail is spread, and the bird's back is turned toward its mate. The function of this display is not yet clear. It is given most often when the mate of the reactant approaches closely, and it appears to be some form of appeasement display. Van Tyne and Berger (1959), Selander and Giller (1960), and Andrew (1961) discuss bill-raising as a component of different kinds of display among passerine species.

All these courtship displays have "degrees of expression," which are indicated in part by the intensity of the wing movements. At low intensities the wings are held with the tips slightly drooped to the sides below the level of the rump, against which they are usually folded in the resting position, and they are then quivered slightly. The movement is most conspicuous at the tips of the wings, in contrast to flight-intention movements, which are most obvious at the carpus. Vocalizations may not be given at all. As the tendency to engage in courtship-feeding increases, vocalizations are added, and the wings are held more loosely from the sides (slight extension of the forearms) and are quivered more conspicuously. In the extreme expression, the vocalizations are loud and constantly repeated, the forearms are extended from one-half to three-fourths their full reach, and the wings are fluttered by rapid strokes of the humeri. Although the hands never seem to be maximally ex-

tended during these extreme wing-flutters, the wing patches are quite visible and make conspicuous "flashes" as they pass through the arcs described by the moving wings.

Wing movements are not a part of the usual intraspecific agonistic displays of the Northern Shrike, but spreading of the tail and ruffing of the feathers on the dorsum are. Occasionally when a subordinate, caged bird is hard pressed by a dominant individual, it will assume a juvenile posture with the feathers fluffed out and its head sunk deep into the furcular region, whereupon it quivers its wings and utters the food-begging whine. This reaction probably is not normal but occurs only in confined places such as cages. The fact that wing movements are not usually a part of the intraspecific hostility of the Northern Shrike should be borne in mind when considering the descriptions of hostility toward other species.

Typical observations.—8 June 1959, 5:00 PM. The following observation was made at a nest in a stand of willows on an alluvial fan at the northeast corner of Lake Peters, Alaska. Six eggs were present. When first observed, the female, an immature bird, was perched atop a willow a few feet from the nest. She was singing a repetitious song phrase and occasionally fluttering her wings and giving voice to the *waik* food-begging whine. In a few seconds, the adult male flew to her from an undetermined point lower down on the fan and fed her a bit of meat. Both birds fluttered their wings during the feeding. The male then departed, and the female flew to the nest and soon sat on the eggs.

15 June 1959, 3:00 PM. This observation was made at a nest on the east side of Lake Peters. Eight recently hatched young were in the nest. The male was perched quietly in the top of a willow about 10 yards away from the nest, while the female was sitting on a branch about a foot from the rim of the nest. The female kept up a continual food-begging display for about five minutes, with frequent whining and the wings constantly quivering. Suddenly the male flew away about 30 yards downhill to a mouse carcass hung in a fork two feet above the ground. As he flew, the female turned on her perch, keeping her head pointed in his direction, her whines became louder and more rapidly repeated, and her wings were quivered more. The male stripped off a piece of meat from the carcass and then flew with it in his beak back to his first perch, where he looked down intently at the female or at the nest. The female's begging increased still more, as her wings were extended farther from her body and were fluttered through a wider arc than previously. In a few seconds, the male flew down from his perch, dropping low just over the ground to land in the lower branches of the nest tree. Then by jumping from branch to branch he worked his way up to the nest. He jumped right past the food-begging female to the rim of the nest, where he immediately fed one of the young. He remained on the rim of the nest, looking down at the young and poking his beak among them, apparently waiting for a fecal sac to be voided. During this time, the female was actively flitting about in the branches just above the nest, making a hollow *beek* sound and still quivering her wings. After a few more seconds, the female came to the nest and settled on the young while the male was still on the rim. The male then flew back to his original perch.

29 January 1961. Observation on the initial introduction of a captive, wild-caught adult female to a captive, hand-reared immature male. The male had been on a 20-hour photoperiod for 28 days and was sexually motivated; the female had been on an 8-hour

photoperiod for several months, but she too showed some behavioral signs of sexual recrudescence. At 8:15 PM the female was placed in the room where the male was kept. Bits of meat were present in the food dish. The female flew to the back of the room and landed on a high perch, where she sat looking around. She appeared neither frightened nor aggressive, but sat quietly in a normally relaxed posture. The male did not attack her or make any vocalizations, but he flew to a perch about 6 inches directly above her and sat looking down at her for a couple of minutes with his head lowered below the level of his feet and his tail pointing obliquely up into the air. The female did not move away or display aggressively; instead, she sat with her head pointed up at the male but sunk deeply into the furcular region. Soon the male flew several feet to the front of the room, where he sat looking at the female in a mildly hostile posture with his crown raised and the feathers on his back slightly ruffed. The female began looking down at the food dish, soon flew to it, and ate several bites while perched on the rim of the dish. Then she flew back to her previous perch, but almost immediately she dropped down again, this time to the water dish, where she drank. While she was at the water dish, the male suddenly swooped down over her uttering the aggressive, rattling *aak, aak* call, but the female continued to sit calmly on the dish without displaying. Then she hopped over to the food dish and ate some meat. Again the male dived over her screaming, but she continued eating as though he were not even in the room. Soon the female flew back up to her perch, where she wiped her beak, roused, and began preening her plumage. The male then hopped to a special perch where he sang a lot of the time (his chosen nest-site), assumed a sleeked upright posture with his beak pointing up and his tail fanned out, and quivered his wings violently, keeping his back to the female and uttering a series of *wuut* notes. The female continued to perch quietly. Then the male flew down to the food dish, picked up a bite of food in his beak, looked up at the female, quivered his wings and uttered *wuut*, and then flew straight up to her side, fluttering his wings and uttering *wuut* over and over. He offered the piece of meat to the female, who took it immediately without making a sound or moving her wings. This first feeding occurred 15 minutes after they had been introduced. In the next half-hour the male fed the female six more times. Each time his wings were quivered or fluttered, but no sound was made. The female did not move her wings or vocalize during these first encounters.

HUNTING TACTICS

General description.—The Northern Shrike hunts in two basic ways. Most commonly the shrike perches on some high vantage, usually the upper branches of the tallest tree in the area, from which it keeps a vigilant watch for suitable prey moving on the ground or in the air below. Once the quarry is chosen, the shrike suddenly drops straight down from its perch and flies just above the surface of the ground, often using concealing landforms to remain hidden from view of the quarry as it approaches. Thus, it apparently attempts to catch the prey by surprise. This method of hunting is quite reminiscent of the tactics used by accipiters (see Tinbergen, 1946, for details about *Accipiter nisus*).

Alternatively, the shrike may move actively about on the ground, through brush, or among the branches of trees in apparent attempts to flush quarry into flight. This type of hunting is more likely to take place after the shrike

has failed to effect a capture by the first method, and the prey has sought cover.

Birds are sometimes pursued actively in flight, and occasionally they are caught in the air; but I believe aerial capture is exceptional and that birds are usually taken by surprise while perched on the ground or in bushes and in trees. The Northern Shrike catches birds in its feet, just as an accipiter does; but it kills them—and all other vertebrate prey—by biting into the neck and severing the cervical vertebrae, just as falcons do (see Cade, 1960). I have never seen an exception to this method of killing, and Thielcke (1956) also calls attention to the fact that this shrike always kills with its beak.

A shrike does not usually grab a rodent in its feet, because it is likely to be bitten if it does so. Instead, it jumps and dances erratically about the rodent, reaching in when the advantage is right to deliver a series of quick bites at the neck. A small mouse weighing 20 to 25 grams is easily killed in a few seconds, but larger rodents weighing 50 grams or more may take several minutes and many bites.

When hard pressed by a shrike, small birds always seek the protection of dense brush or thickly branched trees, in which they "freeze" and from which they are reluctant to leave. Once inside a bush or among the branches of a tree, small birds are relatively safe from a shrike, even if the predator plunges right among the branches with them, for a small bird like a chickadee or sparrow by hopping from branch to branch can easily avoid the shrike, which cannot maneuver so fast or so adroitly through the dense tangle of branches. Only if a "frozen" sparrow does not see the shrike approach, or if it essays to fly out of the tree across open terrain to an adjacent patch of cover, does the shrike have a possibility for effecting a capture.

I have seen one of my trained shrikes stalemated for half an hour in an isolated spruce tree with a flock of six to eight Black-capped Chickadees (*Parus atricapillus*), which were often perched only one or two feet away from their antagonist. The chickadees, constantly uttering the *chickadee-dee-dee* call, would work their way up to the top of the tree pursued from branch to branch by the shrike. When they finally reached the top and it seemed that the shrike would at last have a chance to pounce on one, instead of flying off to an adjacent tree, the chickadees one by one, dodged around the shrike and started working their way back down the tree, with the hapless shrike still in pursuit.

It was during these encounters with quarry holding to dense cover that I first became aware that shrikes use special wing movements under such circumstances in apparent attempts to flush the prey into a more vulnerable position. Under such circumstances, the hunting shrike often flits about through the branches with bobbing and twisting movements of the tail and

with the wings quivering or fluttering. Some of these movements are quite clearly flight-intentions, but others are not. Often the wings are quivered only slightly, just as in low intensity courtship-feeding. The movements are exactly the same. In a more intense expression, the wings are extended from the sides and are fluttered up and down rapidly, during which the wing patches describe conspicuous flashing arcs. Again the actions are indistinguishable from high intensity food-begging movements. The tail is also spread and closed rapidly, a movement which is unlike the aggressive spreading of the tail, in which the tail is held in the spread position and is associated with ruffed plumage. In the most intense expression of this behavior, the wings are greatly extended from the body but are drooped so that the tips of the primaries are well below the axis of the body, and the tail is maximally spread. As the tail is spread, the wings are swept forward, during which there is a conspicuous extention of the hands, producing a maximum exposure of the white areas on the primaries. Then the wings are snapped back to a drooped, half-extended position, and the tail is closed. One complete cycle of these movements produces a conspicuous flash of the wing patches and of the white areas on the tail.

Similar movements are performed on the ground during attacks on large rodents. In these encounters the tips of the primaries may actually touch the ground as they are swept forward. The wings are never held high over the back of the shrike, although sometimes they are extended horizontally from the sides. Forward sweeping of the wings with extension of the hands is especially likely to occur when the shrike is attacking a rodent near the maximum size it can kill (80 to 100 grams). No vocalizations usually accompany these movements, except when aggressive tendencies are also present, as may be the case when a vigorous rat fights back. In that event, ruffing of the dorsal feathers also occurs.

Typical observations.—7 June 1959 at the south end of Lake Peters, Alaska. As I was walking along one of the channels of Carnivore Creek, a sudden commotion at the mouth of the creek 50 yards away caught my attention. An adult shrike was chasing a female Lapland Longspur (*Calcarius lapponicus*) along a zigzag course one to two feet above the ground. The shrike followed every twist and turn of the longspur, keeping just behind her tail. The birds flew upstream toward me. Then a male longspur descended from the air above and joined in the flight, uttering alarm notes and flitting about above the shrike. The latter did not take its attention away from the female longspur. When about 20 yards from me, the shrike struck at the female longspur—it was not possible to tell just how—and she fluttered down into some clumps of grass about one foot high on the bank of the creek. There were also some large rocks and mounds of dirt that afforded hiding places for the longspur. The shrike hovered over the spot where the longspur disappeared and then dropped to the ground. The shrike began hopping about in an excited manner from grass clump to grass clump, up onto rocks and mounds of dirt, clinging momentarily to stems of grass, back to the ground, maneuvering all through the area

where the longspur had evidently hidden. Unfortunately, I did not pay close attention to the wing movements during this episode, but the wing patches and white markings on the tail were definitely flashing much of the time. All this while the male longspur kept flitting about, calling in the air above the shrike. In crossing the creek to approach closer, I was forced to divert my attention momentarily from the action of the birds, and when I was able to look up again, the shrike was flying heavily away with a longspur in its feet. It flew a straight course for a quarter of a mile to a small patch of willows on a lateral moraine along the east wall of the valley. While in flight the shrike was assailed by a Water Pipit (*Anthus spinoletta*). I marked the spot where the shrike landed, and in a few minutes I found the prey already decapitated and wedged into the forked branch of a decumbent willow, lying on the ground. It was a male longspur! Apparently, not being able to find the female, the shrike had turned suddenly on the pestering male and caught him instead.

21 August 1958 at Jago Lake, Brooks Range, Alaska. Three post-fledgling, juvenile shrikes—probably siblings of a late brood—had been hunting for a week about our camp at Jago Lake and in the willow brush growing on alluvial bars in the flood plain of the Jago River. These birds evidently had been attracted to the area by an unusual swarm of grasshoppers, which appeared in mid-August. The shrikes were observed repeatedly taking these insects from the tundra vegetation. On this date, one of the shrikes was observed perched in the top of a willow growing in the river bottom. Twenty yards across the river there was a steep slope with large boulders protruding from the tundra mat of mosses, dwarf willows, heaths, and other decumbent shrubs. Suddenly the shrike flew across the river and landed on top of a rock. Orienting itself horizontally, the shrike looked down intently at the ground and then simultaneously fluttered its wings and spread and closed its tail. This act was repeated several times in quick succession; then the shrike jumped to a spot on the ground about three feet away and snapped up a grasshopper in its beak. The shrike flew back up onto the rock and ate the insect there. Since the wing patches and the light markings on the tail of juvenile shrikes are not pure white, no striking flashes were produced by movement of the wings and tail on the rock, but the behavior was typical of movements which I was later to see executed many times by my tame shrikes, and it was followed, in this case, by the immediate capture of food.

24 June 1961 at Lake Peters, Alaska. Observation on three hand-reared young. These young shrikes had been removed from their nest at the age of 13 to 14 days and were 22 to 23 days old on this date. They were kept in a small tent with a floor space of 6 by 6 feet and a ceiling height of 6 feet at the apex. A willow bush was provided for perches. At this age the young were actively hopping about in the branches of the willow, but they could not make sustained flights of more than a few feet. Numerous blowflies and other small, flying insects became trapped inside the tent and spent their time crawling about on the walls and ceiling. One of the young shrikes was observed watching intently all the moves of a blowfly crawling on the tent about two feet away from the bird. This fly frequently buzzed around inside the tent. Whenever the fly came within 6 to 8 inches of the shrike, the bird sleeked its plumage, assumed a horizontal position facing the fly, and quivered its wings, as in low intensity food-begging. If the fly came close the shrike also snapped at it. On subsequent days, all three of the young shrikes were seen performing this kind of behavior many times, as they became more interested in stalking and catching these insects. Captures were frequently made.

2 September 1960 at the Manlius School, New York. Large flocks of Chipping Sparrows (*Spizella passerina*), Robins (*Turdus migratorius*), and Starlings (*Sturnus vulgaris*) were foraging on the athletic fields. I walked up close to a group of sparrows, carrying

one of the trained shrikes (Green, a female weighing 65 grams) in the portable cage. At a distance of 10 yards, I released the shrike, but she did not pursue the sparrows; instead, she returned immediately to the cage looking for food, putting many of the sparrows to flight as she did so. Finally, she flew out again and landed on some bleachers back of a baseball diamond. A dozen sparrows were feeding under the bleachers. On seeing the shrike, some of these sparrows flew up and landed a few feet away from her on the top of a bleacher. The shrike immediately sleeked her plumage and assumed a horizontal position with her head pointing toward the sparrows. Then she began quivering her wings and hopping toward the sparrows along the back of the bleacher. The sparrows did not get frightened and did not take flight until the shrike was less than a foot away and almost close enough to grab one. The sparrows then flew toward a stand of second-growth aspen, and the shrike chased after the birds but soon lost them in the dense brush.

20 September 1960 on a vacant lot in Manlius, New York. A flock of House Sparrows (*Passer domesticus*) was feeding on the ground in a vegetable garden. I approached slowly with a trained shrike (Red, a male weighing 75 grams) in the portable cage, but the sparrows became frightened, and one by one they started flying up into a nearby spruce tree. The shrike immediately sleeked his plumage, assumed a horizontal position on his perch inside the cage, and quivered his wings. I released the shrike 10 yards from the spruce tree. He flew straight up into the tree to a height of 15 feet and caught an immature sparrow sitting on an outside branch. I feel certain the sparrow did not see the shrike approaching. The shrike fluttered to the ground with his prey, and there holding the sparrow by its wings, he bit its neck several times until it was dead.

22 October 1960 in the backyard of my residence in Manlius, New York. Carrying Green in the portable cage, I approached a Black-capped Chickadee foraging in the lower branches of a leafless tree about 15 feet above the ground. At a distance of 20 feet, the shrike saw the chickadee and reacted with the characteristic sleeking of the plumage and assumption of a horizontal position on her perch. Her wings were then quivered several times in rapid succession. The chickadee paid no attention to our presence. I opened the cage door; the shrike dashed out and grabbed the chickadee before it had a chance to move off the branch. She carried the prey in her feet to the roof of a nearby garage, where she killed it by biting into its neck. Then she flew with the chickadee to an apple tree, where she hung it by the neck in the forks of a branch.

22 October 1960 at the Manlius School, New York. I took Red to the athletic field, where I released an adult male House Sparrow for him to chase. There was a long "tail-chase" all about the field, following a zigzag course of about 300 yards. Finally the sparrow escaped into a low hedge at the side of the gymnasium. The shrike perched in the branches of a tree about 10 feet above with his head pointed down below the level of his feet and his tail pointed diagonally upward. His tail and wings were repeatedly moved in flight-intentions. I ran up and put the sparrow out of the hedge several times. The shrike was very eager, but he missed the sparrow each time it was in the open. Finally the shrike flew into the hedge with the sparrow and hopped from branch to branch in pursuit, but the sparrow easily kept ahead of him to the end of the hedge at the corner of the building, where it flew quickly around the corner and disappeared from my line of sight with the shrike immediately after it.

I do not know what happened after that for several seconds, but the sparrow somehow slipped away from the shrike. About 50 yards up a hill from the gymnasium I contacted the shrike again. He was perched atop a dense thorny bush with three, excited Black-capped Chickadees flitting about in the lower branches. Periodically the shrike sleeked down his plumage, assumed a horizontal position, quivered his wings, and then jumped

down among the branches where he hopped about after the chickadees. While pursuing the chickadees from branch to branch, the shrike often extended his wings from his sides and fluttered them, at the same time spreading and closing his tail. The chickadees were so reluctant to leave the cover that even when I crawled in under the bush and tried to shake them out they would not fly away. Often one of the chickadees was no more than a foot away from my face. My close presence seemed to spur the shrike to renew his attacks from above with increased vigor—especially the extent to which his wings were fluttered—but in more than 5 minutes of repeated attempts, he never got really close to one of the chickadees. Suddenly the shrike flew away. Squatting under the bush, I could not see where, but it was evidently a long distance, because the chickadees soon essayed to fly across an open weed field. I lost contact with the shrike for about 5 minutes.

When next encountered, the shrike was in some tall elms behind the gymnasium, attacking a Blue Jay. The jay, putting up surprisingly little defense, kept moving away from the shrike and uttering very metallic, ravenlike croaks as it flitted from branch to branch. Then two more jays appeared, and the shrike chased after them all with abandon, fluttering his wings whenever he approached one of the jays closely. The jays soon left. In the brush below the trees, there were several Robins, and the shrike next dived down and chased these birds out of the area. In the same patch of woods, there were also two Downy Woodpeckers (*Dendrocopos pubescens*) foraging on the trunks of the larger trees. After returning from the Robins, the shrike flitted up into the branches near the woodpeckers and started the characteristic bobbing antics with his wings quivering or fluttering. Then he flew at one of the woodpeckers, which avoided his attack by dodging around to the other side of the trunk. The shrike then sat on a branch bobbing up and down, quivering his wings, and spreading and closing his tail for several seconds before attacking again. The result was always the same: the woodpeckers easily avoided him by moving around on the tree trunks. Then another Robin flew by just over the tree tops, and the shrike left the woodpeckers to chase after the Robin. This flight ended about 300 yards away on a building, where the shrike landed on top of a tall smoke stack after losing the Robin in some shrubbery around one of the dormitories. I followed after and arrived just in time to see the shrike chase a feral pigeon around the building. The pigeon spiraled up high, easily leaving the shrike behind. Red returned to the top of a nearby spruce tree, and I finally called him back into the cage almost an hour after his initial release.

30 October 1960 on a vacant lot in Manlius, New York. After an unsuccessful attempt to catch a Black-capped Chickadee, Green perched 20 feet above the ground in the top of a leafless tree. Standing 20 yards away, I released an adult female House Sparrow, which started flying toward another tree about 50 yards away. The shrike immediately chased after the sparrow and soon caught up with it. Just as the sparrow was approaching the tree, the shrike made a determined but unsuccessful attempt to snatch the sparrow in flight. The sparrow fled into the central branches of the tree, where it sat cowering. Just as the sparrow was entering the tree, the shrike abruptly changed course and shot straight up to the topmost branch of the same tree. She sat motionless in an upright position with her head cocked down, obviously looking intently at the sparrow. I had the distinct impression that the sparrow did not see where the shrike had gone. At any rate, the sparrow continued to sit motionless on its branch in the central part of the tree. A few seconds later, the shrike suddenly plummeted straight down through the branches and grabbed the sparrow with her feet before the prey could move. The shrike sat right where it had caught the sparrow and began biting into its neck. The sparrow uttered a series of squeals (a typical reaction of House Sparrows when caught by a shrike), and almost at once three other House Sparrows and two Downy Woodpeckers flew into the

tree and started mobbing and scolding the shrike. When the shrike had first grabbed the sparrow, she also had caught hold of a spray of twigs in the same foot. During the mobbing, the captured sparrow managed to struggle loose, but the shrike continued holding onto the spray of twigs, struggling with it and trying to fly away with it, acting as though she still held onto the sparrow. In the meantime, the sparrow escaped with the other three, apparently before the shrike realized she no longer held her prey. The shrike then pursued the two pestering woodpeckers, which retreated into the upper branches of the tree. Again, these birds easily eluded the attacking shrike by dodging around on the trunks. The shrike kept up a series of short attacks from branch to branch, and between attacks while perched on a branch watching the woodpeckers, she fluttered her wings conspicuously and spread and closed her tail. The woodpeckers were just about as aggressive as the shrike and made short advances toward her, scolding and also fanning out their wings. The interaction between these birds continued for more than 10 minutes, before I was finally able to entice the shrike down to her cage for a bite of meat.

17 December 1960 in a large outdoor flight cage. An immature laboratory rat weighing 77 grams was placed in the cage with Red. The rat moved about normally exploring the floor of the cage. The shrike sat in an alert, horizontal position four feet above, looking intently down at the rat and following its every move by appropriate turns of his head. Then his tail began flipping down and up, followed by a number of flight-intention flicks of his wings. The flight-intention flicks were interspersed with brief periods of wing-quivering. Then the shrike dropped onto the ground and hopped rapidly up behind the moving rat. The rat stopped briefly in a corner, and the shrike jumped in close to deliver a quick bite at the neck, but the rat turned on the shrike, warding the bird off with its forelegs. The shrike jumped back a few inches and stood in an upright posture looking at the rat and uttering *jaa* calls. The rat began to move away; then the shrike started a series of quick jumps and flits around the rat, fluttering his wings repeatedly and giving the *jaa* call. Often, the shrike moved in close and struck toward the rat's neck with his beak, being careful always to jump back quickly. Between encounters, the shrike flew back up to a perch to watch the rat. There, looking down intently, the shrike quivered his wings and called. After several such attacks, the shrike flitted to the ground and hopped toward the rat, which was now cowering from several hard bites in the neck. As the shrike approached closely, he slowed down, assumed an erect posture with the feathers of his neck and crown ruffed out aggressively. His tail was spread and depressed toward the ground, and his wings were extended and drooped so that the tips of the primaries were near the ground. Then, as the shrike made quick hops at the rat, he swept his wings forward with maximal extension of the hands, producing a conspicuous flashing of the wing patches. As he flicked his wings back to a half-folded, drooped position, the shrike also jumped back away from the rat. These maneuvers were repeated several times. The rat did not move. Then the shrike hopped quickly to the rat again and bit into its neck with a long hold of several seconds. This bite caused the rat to drag itself away sluggishly, and the shrike quickly followed the struggling rat, delivering a series of hard bites to the neck. After 4 minutes and 50 seconds from the time of the shrike's first bite, the rat lay on its side, kicking its hindlegs spasmodically. The shrike sat quietly nearby, occasionally nibbling at one of the twitching feet of the rat. It took the shrike a total of 117 grabs at the neck to kill this vigorous rat.

HOSTILE REACTIONS TO LARGE ANIMALS

General description.—In this category I have grouped together the responses of shrikes to a variety of different species and under varying cir-

cumstances—potential nest predators, competitors for food, non-predator species too large to serve as prey, strange objects, stuffed hawks and owls. The one feature common to all these animals is that they are too large to be killed by shrikes. The wing movements used by shrikes in encounters with these species are exactly the same as those described previously in the section on hunting. While there is no absolute difference between the responses of a shrike to a large prey animal—for instance, an 80-gram rat—and a potential predator or competitor for food such as a Kestrel (*Falco sparverius*), there are average differences in the frequency with which the various kinds of wing movements occur in the two situations. When reacting against a species too large to kill, the shrike is more prone to employ the extreme "wing-flashing" movement, in which the wings are extended, drooped, and swept forward with maximal extension of the hands. Moreover, the aggressive *jaa* and *aak* calls are given frequently during these encounters, and the displays involving wing movements are often interposed by true hostile displays, such as are used in intraspecific aggressive encounters, which employ ruffing out of the feathers on the dorsal surfaces and extreme spreading of the tail. These aggressive, ruffed-out postures rarely occur during hunting attacks and then only when the quarry is very large and potentially dangerous (large rodent).

Typical observations.—6 July 1959 on a brush-covered island along the middle reach of the Colville River, Alaska. A recently abandoned shrike nest was found at the edge of a dense stand of willows averaging 15 feet in height. Both adults and three or four young were still present in the immediate area. The nest, which was situated about 8 feet above the ground, had been ripped apart. Most of the outer structure of sticks had been torn or shaken loose, and ptarmigan feathers from the inner, felted layers were strewn about on the ground under the nest over a radius of 6 feet or more. Although all the young present were fledged, the adults still protected the nest, following me to the site and sitting nearby scolding with the *jaa* call and ruffing out the feathers on their backs and crowns. While I was examining the nest, the adults suddenly turned their attention from me and flew 30 or 40 yards away through the brush, uttering loud and persistent *jaa* screams, which continued all through the subsequent action. I could see the shrikes diving from the willows toward some animal on the ground and then quickly darting back up into the branches. There they hesitated a few seconds, looking down, screaming, bobbing up and down, spreading and closing their tails, and fluttering their partly extended wings before attacking again. The wing-fluttering was interspersed with typical wing-flicks of flight-intention. The extreme "wing-flashing" movement was not seen. As the shrikes continued attacking, they moved in my direction toward the nest. Suddenly a Red Fox (*Vulpes fulva*) appeared in a clearing between two willows. The fox stopped about 10 yards away when it saw me; then it turned around and trotted off casually with both shrikes still diving over its back and screaming. It seems likely that this fox had visited the nest previously.

26 October 1960 in the Episcopal Church Cemetery, Manlius, New York. Following an unsuccessful flight after a House Sparrow, Red flew up into the main branches of a tall elm, where an adult Gray Squirrel (*Sciurus carolinensis*) sat husking a nut. The shrike showed immediate interest in the squirrel, which began to chatter when the bird

flew into the tree. The shrike sat several feet above the squirrel, intently looking down at it and flipping his tail down and up for several seconds. Then the shrike flew down and hovered just over the squirrel's head. The squirrel became agitated and started scolding. The shrike flitted back to a nearby branch and sat there in a horizontal position, spreading and closing his tail and fluttering his wings. No vocalizations were given. Then the shrike dived over the squirrel's head to another branch. The squirrel flattened out on its branch. The shrike next landed on the same branch with the squirrel and advanced toward it by a series of short hops. As he approached, the shrike extended his wings horizontally and fluttered them periodically. When the shrike was within two feet of the squirrel, he drooped his wings and swept them forward in conspicuous flashing movements. At the same time his tail was spread and closed. As soon as the squirrel moved a little, the shrike quickly flitted away to a close branch. Variations of this attack and retreat were repeated for about 5 minutes, until a sparrow flew by diverting the shrike's attention from the squirrel. Later, in the same area, the shrike also had a similar encounter with two subadult Red Squirrels (*Tamiasciurus hudsonicus*). The same wing movements were again very much in evidence. The shrike pushed his attack a little more vigorously with these smaller squirrels, actually striking one and causing it to fall several feet through the branches before it regained a hold. Both these squirrels finally escaped by running into hollows.

20 February 1961 in a large, indoor flight room. An adult, male laboratory rat weighing 300 grams was placed in the room with Red and an adult female shrike (Blue). Both birds immediately fixed their attention on the rat and followed its every move for more than 10 minutes. They uttered no vocalizations, and their plumages were sleeked at all times. The shrikes assumed a horizontally crouched posture with their heads slightly lower than their tails. Their heads were cocked downward with one eye always following the rat, which moved about actively on the floor below. In this posture, the shrikes hopped from branch to branch slowly following the rat, but not once did either bird attempt to dive at the rat or strike at it. There were, however, many typical flight-intention tail-flips and wing-flicks, and several times Red also quivered his wings slightly. Blue also quivered her wings once or twice, but she was less responsive to the rat than Red was, and at the end of 10 minutes Blue was no longer paying close attention to the movements of the rat; but Red's attention was still completely fixed on the rodent.

Then I removed the rat briefly, killed it by concussion, and threw it back on the floor of the room. The rat made a few convulsive kicks of its hindlegs for several seconds. Red's reaction was immediate. He hopped down to a perch just above the rat and gave many intention-movements to jump down by the rat, but he appeared reluctant to do so. During all the time the rat was lying on the floor, the shrike never approached closer than about 18 inches; but for 5 minutes he was in close attendance. During this period the shrike fluttered his wings many times whenever he approached the rat closely. Especially when he moved close to the rat, the fluttering changed into the more conspicuous "wing-flashing" movement previously described. Sometimes, after several flashes, the shrike stood erect and motionless with the wing nearest to the rat drooped and more extended than the opposite wing, and his tail was spread and canted to the same side. The shrike appeared definitely reluctant to touch the rat, and I had the distinct impression that the bird was "trying to test" the rat to see whether or not it would move. Blue did nothing but sit high above and watch. After 5 minutes, Red's interest in the rat began to wane, and he started flitting up to higher perches, then returning briefly to display near the rat, soon flitting up again to sit near Blue. For three more minutes he con-

tinued to show some interest in the rat, but the wing-fluttering became subdued and finally merged into the low intensity quivering.

After Red's response had subsided, I picked up the rat and hung it by its neck in the forks of a branch three feet off the floor, in the typical way a shrike "impales" its prey. Again, Red's response was immediate. Showing no signs of fear or reluctance to approach, Red jumped right up to the rat and at once bit into its neck several times. Then he started trying to strip the skin around the eyes of the rat—the usual way a shrike begins to dismember a carcass for feeding. This response was in marked contrast to his cautious and hesitant behavior toward the rat when it was lying on the floor.

4 March 1961 in the same room. I placed a stuffed male Kestrel, mounted in a normal sitting posture, on a slanting perch one foot off the floor in the room with Red and Blue. Blue remained quiet on a high perch, only looking down at the dummy, but Red at once assumed an aggressive ruffed-out plumage with his tail widely spread and commenced a series of loud, rapidly repeated *aak* notes. At first, he flitted about in the upper branches, scolding and keeping his eyes fixed on the Kestrel. Occasionally he gave flight-intention movements. After about two minutes, he jumped down onto some lower branches, still ruffed out and screaming. Now and then he assumed a brief upright position, during which he quivered his wings as he looked down at the dummy. Finally he jumped to the slanting perch on which the dummy had been placed and advanced by short hops down the perch toward the dummy. His wings were quivering slightly. The shrike's movements on the perch caused the dummy to fall over on its side on the floor. At first the shrike was startled and jumped back on the slanting perch; but he then immediately began advancing toward the dummy again, no longer ruffed out and no longer vocalizing. The approach became cautious. When the shrike was about one foot from the dummy, he fluttered his partly extended wings, bobbed up and down, spread and closed his tail several times. Then he jumped back from the dummy, only to begin approaching again. Variations of this approach-and-retreat sequence were repeated several times. Usually the wings were fluttered on close approaches, and several times they were also flashed. Finally, the shrike hopped down onto the floor by the Kestrel and fluttered and flashed his wings and tail around the dummy for a minute or more. In about 5 minutes, the shrike's response began to wane, and he finally returned to the upper branches, although still looking down frequently at the dummy, occasionally ruffing out a bit and even uttering the scolding *aak* note.

DISCUSSION

The accounts presented above have been selected from dozens of similar records in my notebooks since 1958 and are sufficient to show that quivering, fluttering, and "flashing" movements of the wings are often associated with the hunting activities of Northern Shrikes and with their reactions toward potential predators or other large species. It is not surprising that little has been reported about this kind of behavior by previous investigators; the Northern Shrike is not a commonly observed bird, and it remains one of our least-studied Holarctic species. Miller (1931) in his account of the natural history of North American shrikes makes no mention of this kind of behavior; nor does Thielcke (1956) in his excellent analysis of the hunting behavior of the nominate race in Germany refer to such habits. Of the works I have reviewed, only Zimmerman (1955:205) records similar behavior based on his

observations of wild shrikes in Michigan in the winter: "Near Imlay City, Michigan, December 5, 1954. I watched a subadult Gray Shrike fly from its perch on a roadside wire to a tree near a chicken yard where numerous House Sparrows (*Passer domesticus*) were noisily feeding on the ground. Apparently attempting to startle the sparrows into flight, the shrike began excitedly jumping about—from branch to branch, from the tree to an adjacent wire fence or to low telephone wires and back to the tree again—all the while flopping its tail and repeatedly spreading its tail and wings. As I followed the rapid action (with difficulty) through the telescope I was continually reminded of a Mockingbird's (*Mimus polygottos*) 'wing-flashing.'" Zimmerman's comment on the difficulties involved in making his observation substantiates my own field experiences and confirms the usefulness of making observations on tame or trained birds under partly controlled and partly natural conditions.

Although it is possible to conclude from the data presented here that these special wing movements are definitely associated with hunting and with hostile reactions toward other species, the function and the biological significance of this kind of behavior are open to several possible interpretations. as previously discussed by Selander and Hunter (1960) and by Hailman (1960) for wing-flashing of the Mockingbird.

BIOLOGICAL SIGNIFICANCE OF THE WING MOVEMENTS

Even though I have only once seen wing-fluttering by a wild shrike followed by the immediate capture of food—an association which Hailman (1960) has been able to establish by statistical analysis for wing-flashing by the Mockingbird—the fact that these movements occur so frequently during hunting forays leads to the inference that they serve a useful biological function. Moreover, the specific situations in which the movements occur during hunting—that is. when the prey has taken a stand in dense cover—strongly suggests that the wing and tail movements produce a startling effect that sometimes flushes the prey into flight or into moving sufficiently to make itself more vulnerable to capture. This conclusion is the most reasonable one that can be drawn from the present observations.

Similarly, intimidation and distraction seem to be the functions of these wing movements when they are directed against a possible predator or other large species. To this extent, the wing movements of shrikes also appear to function in ways analogous to the hostile use of wing-flashing by Mockingbirds (Selander and Hunter, 1960), but there is no indication that they also function as social displays in intraspecific aggressive encounters, as these authors claim for the Mockingbird.

Selander and Hunter (1960) concurred with Sutton (1946) that wing-flashing by the Mockingbird indicates a state of wariness, suspicion, and

distrust. These are frankly anthropomorphic adjectives that also apply in a descriptive sense to the motivational state of the Northern Shrike when it is engaged in wing movements. The behavior seems to indicate that the shrike is hesitant or unsure about what action to take, especially when it has been thwarted in attempts to capture prey, which has escaped into safe cover, or when confronted by some strange or unusual encounter with another animal (a rat too large to kill), or a predator which does not fly away (stuffed hawk). There may also be an element of exploration or testing involved. Rand (1941) expressed a similar view about the "snake-display" of the Curve-billed Thrasher (*Toxostoma curvirostre*). (Although Rand's description is not explicit, the "snake-display" may be a form of wing-flashing.) For the moment it is impossible to describe the internal factors precisely, nor does it seem more heuristic to resort to ethological conceptualizations of the possible internal motivations involved (see, for instance, Hinde and Tinbergen, 1958).

COMPARISON BETWEEN SHRIKE AND MOCKINGBIRD

Pattern of the wing movement.—Hailman (1960) presents the best available description of the form of wing-flashing by the Mockingbird. The bird is usually standing on the ground in a normal body position with its head forward when the wing movements are given. The two wings are opened simultaneously in a series of distinct motions or "hitches," which vary from one to five in number. The direction in which the wings are opened also varies from horizontal extension to nearly vertical over the back. As the wings are hitched open, the white patches are flashed; then the wings are brought back to the body in one, quick, uninterrupted motion. According to Hailman there are no movements of the wings intermediate between wing-flashing and other characteristic, special wing movements of the Mockingbird. Hailman makes no mention of movements of the tail, which is conspicuously marked with white on the outer feathers in a manner similar to the markings of the Northern Shrike. Selander and Hunter (1960), however, mention simultaneous fanning of the tail when a Mockingbird was wing-flashing in response to a stuffed Mockingbird placed in its territory, and a photograph accompanying their article shows a Mockingbird wing-flashing with spread tail near a stuffed Screech Owl (*Otus asio*).

Comparing this brief résumé of wing-flashing by the Mockingbird with the accounts given here of wing movements by the Northern Shrike, it is obvious that the movements used by the two species are not very much alike. The one component of movements by the Northern Shrike that is most comparable to wing-flashing by the Mockingbird is the extreme drooped and forward extension of the wings used against large prey or enemies. Some-

times the wings are extended horizontally during this behavior, but I have never seen the wings of a shrike "flashed" in any position between horizontal and vertical with respect to the body. This lower positioning of the wings may be associated with the fact that the wing patches of the shrike are only conspicuous from the dorsal surface of the wings, whereas the patches of a Mockingbird are equally conspicuous from the ventral or dorsal surfaces.

The shrike does not extend its wings by a series of hitches but usually by one complete outward and forward sweep of the wings. Sometimes the hands may be separately extended near the end of this sweep, producing a single hitchlike movement. The wings usually are not brought back to the body at the end of the shrike's "wing-flashing" before the next flash is given, but instead to a half-extended, drooped position. Moreover, there are definite intermediate wing actions, "wing-quivering" and "wing-fluttering," which are lower intensity expressions of the same tendency and which have a pattern of movements indistinguishable from the quivers and flutters used by shrikes in various mating contexts or in food-begging. The chief superficial resemblance between the wing movements of Northern Shrikes and of Mockingbirds is that the wing patches of both birds produce conspicuous flashing motions when the wings are in action.

Contexts of the wing movements.—There are more similarities between the behavioral contexts in which the two species employ wing-flashing than there are in the form of the movements. Both species frequently use such movements when foraging or hunting, and in both cases it seems likely that the startling effect of the flashing wing patches (and the white areas on the tail?) in some way aids in the capture of food. In addition, shrikes and Mockingbirds both use wing-flashing behavior in various encounters with potentially dangerous or theatening species. There is a suggestion in both cases that the birds are suspicious or distrustful of the animal toward which they are reacting. Thus, the movements of the two birds seem to be clearly analogous and convergent in several respects, but they are not homologous, if one follows a strictly "morphological" criterion of homology.

According to Selander and Hunter (1960) wing-flashing of the Mockingbird also functions as an aggressive, intraspecific social display, although Hailman (1960) seemed doubtful about this point, and the evidence presented by Selander and Hunter is only suggestive. The Northern Shrike does not use such wing movements in intraspecific hostile displays.

DERIVATION OF THE WING MOVEMENTS

General.—To work out homologies in phylogentically relevant patterns of behavior one faces essentially the same problems as in the field of morphological comparison (Lorenz, 1955). On the one hand there is the need to

distinguish between similarities which are merely convergent or parellel and similarities which are homologous and derived from a common ancestry; on the other hand, there is the need to identify transformations that have occurred within a homologous series. As pointed out by Hinde and Tinbergen (1958), morphologists do have the advantage of the fossil record: otherwise, the problems of evolutionary interpretation are the same for the behaviorist as for the morphologist.

There are two fundamental behavioral modalities which seem to have contributed a great deal to the evolution of avian displays and in which special wing movements are conspicuous components. These two are: (1) flight-intention movements (Daanje, 1950; Andrew, 1956), and (2) the food-begging responses of young birds (Andrew, 1961). Both appear to be phylogenetically old characters, and most students of the evolution of bird behavior agree that they have provided many components of behavior which have subsequently been transformed and incorporated into other major modalities of behavior, such as courtship display and agonistic display.

Some significant differences exist between the components of flight-intention and food-begging. Tail-flipping in some form is nearly always associated with flight-intention movements in passerines (Andrew, 1956), but conspicuous movements of the tail are absent in food-begging. Furthermore, the motions of wing-flicking in flight-intention are quite distinct from those of wing-quivering and wing-fluttering used in food-begging, and they probably represent quite different neuromuscular coordinations and central nervous mechanisms.

Origin of wing-flashing by the Mockingbird.—Both the wing-quivering of food-begging (Sutton, 1946) and the wing-flicking of flight-intention (Selander and Hunter, 1960) have been suggested as the original behavioral component from which wing-flashing has been derived. Hailman (1960) points out, however, that the form of wing-flashing does not resemble closely either the wing vibrations of food-begging or the wing-flicks of flight-intention, nor does it resemble any of the other special wing movements in the repertoire of the Mockingbird closely enough to suggest common origin. If none of these pre-existing behavioral components is involved in wing-flashing, then one must conclude that wing-flashing represents the acquisition of an entirely new behavior. Such an assumption goes against the rule of parsimony, and it seems more likely to me that wing-flashing is a highly transformed (ritualized) pattern of behavior derived from previously existing components, which can no longer be identified with certainty. For the present, I am inclined to agree with Selander and Hunter (1960) that wing-flashing of the Mockingbird is probably a ritualized form of flight-intention movements. A more precise analysis of the exact movements used in wing-flashing and

a study of their ontogeny in young Mockingbirds may clarify the problem.

Origin of wing movements of the Northern Shrike.—The wing-quivering and fluttering movements used by a hunting or by a mobbing shrike seem less ritualized than the wing-flashing of a Mockingbird, and for this reason it is easier to speculate about the origin of these movements in shrikes. It seems likely to me that these movements of the Northern Shrike have been derived from food-begging components of behavior. The low-intensity forms of these movements appear identical to the low-intensity forms of wing-quivering and fluttering associated with food-begging and courtship-feeding. Only at the highest intensity does a transformation of movement occur. Wing-quivering and wing-fluttering associated with the pursuit of prey first appear in young shrikes during the fledgling period when they are still partly dependent on their parents and are still begging for food from them. The wing movements used in hunting could, therefore, arise by easy transition or "emancipation" (Hinde and Tinbergen, 1958) from food-begging. Finally, tail-flipping, which is so intimately a part of flight-intention movements, never appears in the context under consideration. Had the lower intensity quivering and fluttering expressions of this behavior been lost in the course of its evolution, so that only the "flashing" movements were now manifested, then one would be faced with the same problem of determining origin as in the case of the Mockingbird.

In conclusion, the Northern Shrike and the Mockingbird provide an interesting example of convergent or parallel evolution of a similar morphological feature (white wing patch), which functions in virtually an identical way in foraging and in hostile behavior. Yet a close study of the form of the movements involved reveals differences which suggest these analogous wing movements in the two species represent transformations of basically unrelated behavioral components.

SUMMARY

The Northern Shrike has white wing patches which are similar to the wing patches used by the Mockingbird for wing-flashing. Field observations on 19 pairs of shrikes nesting in Northern Alaska and on individuals wintering in central New York, and close studies of captive and of free-flying, trained shrikes, revealed that shrikes also use special quivering, fluttering, and "flashing" movements of their wings during hunting forays and in hostile encounters with other species.

Shrikes use special wing movements in many different behavioral contexts: flight-intention, food-begging, courtship display, hunting, interspecific hostility, and in stretching. Like many passerines, shrikes indicate their intention to fly by tail-flipping (down-up type) and by wing-flicking. Typically the wing-flicks are initiated from a normally folded position of the wings, and the movement is most conspicuous at the bend of the wings. Observations of specific instances in which shrikes have shown flight-intention indicate that tail-flipping without wing movements is the lowest intensity of expression of this tendency and that as the tendency to fly increases the wing-flicking becomes more prominent and exaggerated.

The quivering and fluttering of the wings used by male and by female shrikes in the breeding season are concerned mainly with some expression of their tendency to engage in courtship-feeding. Again, specific observations reveal "degrees of expression" of this tendency. Slight quivering movements are the lowest expression; conspicuous fluttering of the partly extended wings accompanied by persistent food-begging whines, in the case of the female, is the strongest expression. When the wings are fluttered in food-begging, the white patches describe conspicuous flashing arcs.

Close observations of tame shrikes trained to hunt out-of-doors show that they often engage in special wing movements when their quarry escapes into dense brush or among the branches of a tree. The same kinds of wing movements are also used when shrikes mob potential predators or other large species of animals. Three degrees of these wing movements can be distinguished: low intensity quivering, medium intensity fluttering, and high intensity "flashing." The first two are indistinguishable from movements also used in food-begging by young or in courtship-feeding by adults. In the most extreme expression of this behavior, the wings are drooped so that the tips of the primaries are well below the axis of the body; then the wings are partially extended and swept forward, a motion which produces a maximum extension of the hands and a conspicuous exposure of the white areas on the primaries. At the same time, the tail is spread widely. Then the wings are snapped back to a drooped, half-extended position, and the tail is closed. A complete cycle of these movements produces a "flash" of the white wing patches and of the outer white areas of the tail.

Although one can conclude that these special wing movements of shrikes are definitely associated with hunting and with hostile reactions toward other species, the biological significance of this kind of behavior can be interpreted in various ways. The specific situations in which movements occur during hunting strongly suggest that the wing and tail movements produce a startling effect that sometimes causes the prey to move from a safe position. Intimidation and distraction seem to be the functions of these wing movements when they are directed against a potential enemy.

These wing movements of the Northern Shrike are not very similar in pattern to wing-flashing of the Mockingbird. Thus, while the movements of the two birds seem to be clearly analogous and convergent in function, they are not homologous on the basis of a strictly morphological criterion of homology. Wing-flashing of the Mockingbird may be a transformation or ritualization of the wing-flicking of flight-intention, whereas the wing movements of the Northern Shrike appear to be less transformed and show a very clear similarity, in the lower intensity expressions, to the quivering and fluttering movements of food-begging.

ACKNOWLEDGMENTS

The field work in northern Alaska has been supported in various ways by the Arctic Institute of North America, by the Office of Naval Research, and by a post-doctoral fellowship from the National Science Foundation. I wish particularly to express my gratitude to Max C. Brewer, Director, Arctic Research Laboratory, Office of Naval Research, Barrow, Alaska, and to his cooperative staff, for their help in providing messing and billeting facilities, clothing, arctic equipment, and logistic support, without which research in arctic Alaska would be greatly hampered. More recently this work has been supported by grant number G-12776 from the National Science Foundation.

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DEPARTMENT OF ZOOLOGY, SYRACUSE UNIVERSITY, SYRACUSE 10, NEW YORK.

16 APRIL 1962